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Development and Metamorphosis of the Planktotrophic Larvae of the Moon Snail, *Polinices lewisii* (Gould, 1847) (Caenogastropoda: Naticoidea)

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Abstract. *Polinices lewisii* from the east coast of Vancouver Island, British Columbia, has been reported previously to have short-lived, non-feeding larvae and juveniles that feed on diatoms and *Ulva* sp. before switching to bivalve prey. However, we found that egg masses of this species from three sites along the southeast and west coast of Vancouver Island, British Columbia, released planktotrophic larvae. Larvae fed *Isochrysis galbana* could be induced to metamorphose at 5 weeks after hatching when cultured at 20–22°C, but repeated attempts to rear larvae to metamorphic competence at 12°C were unsuccessful. Major events of larval development include: bifurcation of the velar lobes, elongation of cephalic tentacles, great enlargement and elaboration of the foot, growth of the larval shell to 2½ whorls, accumulation of black pigment within the epidermis and wall of the gut, and differentiation of the osphradium and gill lamellae. Metamorphosis was induced by sediment from an embayment inhabited by adults, but the active factor was destroyed by autoclaving. Juvenile bivalves had minimal inductive potency. Beginning at 3 to 5 days after metamorphic velum loss, *P. lewisii* drilled and ingested both juvenile bivalves and ostracods; we did not find evidence of feeding on *Ulva*.

INTRODUCTION

Members of the gastropod superfamily Naticoidea are predators of infaunal bivalves and gastropods (see review by Kabat, 1990), which they drill by radular rasping and corrosive secretions from an accessory boring organ at the tip of the acrembolic proboscis (see review by Carricker, 1981). *Polinices lewisii* (Gould, 1847) is the largest extant member of this cosmopolitan caenogastropod superfamily (Marincovich, 1977). The species inhabits fine sediment embayments from the low intertidal to shallow subtidal zone along the west coast of North America. The feeding ecology and digestive physiology of *P. lewisii* have been studied extensively (Bernard, 1967; Reid & Freisen, 1980; Reid & Gustafson, 1989; Peitso et al., 1994). Naticids are also notable for the large size of their foot, which is used for burrowing through surface sediments and for capture and subjugation of prey (Ziegelmeier, 1954, 1958; Fretter & Graham, 1962:572–574; Bernard, 1967; Hughes, 1985). The foot of *P. lewisii* can be inflated to four times the shell volume by uptake of seawater into channels within the foot (Bernard, 1968).

Naticid females deposit their internally fertilized eggs within a benthic egg mass, which is usually a collar-shaped conglomerate of egg capsules and sand held together by a rubbery adhesive (an exception is described by Booth, 1995). Depending on the species, progeny hatch as: (1) swimming, planktotrophic larvae; (2) swimming, lecithotrophic larvae (short-lived relative to the planktotrophs); or (3) crawl-away juveniles (Thorson, 1935; Giglioli, 1955; Amio, 1955; Bernard, 1967). Occasionally, two different life history patterns have been reported for a single naticid species. Thorson (1935) reported direct development for *Natica* (*Polinices*) *catena* (Da Costa, 1778), a species that ingests nurse eggs during embryological development, but Lebour (1936) described swimming larvae for this species. Giglioli (1955) reviewed evidence that *Polinices triseriata* Say, 1826, may hatch as either crawl-away juveniles or swimming veligers. Finally, and of direct relevance to our study, Bernard (1967) reported short-term, lecithotrophic larvae for *P. lewisii,* but Giglioli (1955) predicted planktotrophic larvae on the basis of embryo and egg capsule dimensions measured from preserved egg masses.

Our observations on the life history of *P. lewisii* confirm Giglioli's (1955) prediction of planktotrophic larvae. This result is based on egg masses collected from one location on the west side and two locations on the southeast side of Vancouver Island, British Columbia, Canada. Collections were made during 4 successive years from one of the latter locations. In this report, we describe general aspects of development from larval hatching through metamorphosis into young juveniles.

MATERIALS AND METHODS

Collection and Maintenance of Egg Masses

We examined larvae of *Polinices lewisii* that hatched from egg masses laid in the following localities and years:

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(1) Barkley Sound (west coast of Vancouver Island), summer 1995; (2) Bamberton Harbour, Saanich Inlet (east coast of southern Vancouver Island), summer 1997; and (3) Patricia Bay, Saanich Inlet, summer 1994 and spring to late summer 1995, 1996, 1997. Egg masses were collected during low tides from muddy sand beaches where adults were also found. Egg masses were maintained in aquaria provided with flowing seawater from the recirculating system at the University of Victoria and were aerated continuously from a compressed air outlet until larvae began to emerge.

Larval Culture

Larvae were reared in glass flasks containing 500 mL of seawater that was coarse filtered under vacuum with a Millipore prefilter (#AP 20 047 00). The unicellular alga, *Isochrysis galbana,* was added to the larval cultures at a concentration of 5×10^4 cells/mL for the first 2 weeks and 10^5 cells/mL thereafter. *Isochrysis galbana* was cultured in filter-sterilized seawater enriched with nutrient medium purchased from Fritz Chemical Company (Dallas, Texas). Algal cells were washed before they were added to the larval cultures by centrifuging aliquots of algal culture at approximately 1000 RPM for 7 min, discarding the supernatant, and resuspending the algal pellet in coarse-filtered seawater. Density of algal cells was determined with a hemacytometer. Young larvae were cultured at an initial density not exceeding one larva per 2 mL seawater, but this was gradually reduced by subdividing cultures and removing larvae until a density not exceeding one larva per 10 mL was reached by 3 weeks post-hatching. Larvae were transferred to fresh culture medium every 2 or 3 days by a combination of gentle sieving and hand pipetting. Seawater for culturing larvae was collected once weekly from a rocky coastal promontory in an area subject to strong tidal mixing. It was stored at 12°C in Nalgene carboys and coarse filtered immediately before use. Larvae were cultured at either 12°C or 20–22°C.

Light and Scanning Electron Microscopy

To prevent larvae from retracting into the shell during light microscopical examination and photography, they were anaesthetized in artificial seawater having excess Mg^{2+} and reduced Ca^{2+} (Audesirk & Audesirk, 1980) for periods ranging from 2 hours for hatching larvae to 24 hours for older larvae and juveniles. The cleaned larval shell shown in Figure 1f was obtained by placing anaesthetized larvae in distilled water for 30 minutes, followed by a 6-hour immersion in a 3:10 mixture of household bleach in distilled water. To remove residual, lipid-rich tissues, the shells were taken gradually into 100% methanol, then into a 1:1 mixture of methanol and chloroform for 0.5–1 hr, then back through the methanol series to distilled water.

Larval shells were prepared for scanning electron microscopy according to the method of Hadfield & Strathmann (1990). Cleaned veliger shells and ostracod carapaces drilled by juvenile *P. lewisii* were stored in absolute acetone. They were subsequently air dried, mounted on stubs using nail polish as an adhesive, sputter coated with gold, and photographed with a JEOL SM35 scanning electron microscope.

RESULTS

Larval Development

All egg masses of *Polinices lewisii* that we collected released swimming larvae (Figure 1a, b). When recently hatched larvae were examined microscopically at 1 hour after being placed in seawater containing *Isochrysis galbana* at 5×10^4 cells/mL, algal cells were seen within the larval stomach. Four attempts to rear larvae at 12°C failed to produce metamorphically competent veligers after 3½ months, when the cultures were terminated. However, most larvae cultured at 20 to 22°C were competent to metamorphose at 5 weeks after hatching, some as early as 4 weeks. Larvae that could use their foot for crawling were judged to be competent to metamorphose. Competent larvae tended not to crawl on a clean glass surface, but when cultures were poured through a sieve during the procedure for transferring larvae to fresh culture medium, competent larvae often crawled on the Nitex cloth (64 μm mesh opening) used to construct the sieves. The following description of the pattern and timing of developmental events for *P. lewisii* is based on larvae that were reared at 20–22°C.

Hatching larvae of *P. lewisii* had a bilobed velum, a small foot and shell, and a functional digestive tract (Figure 1a, b). A pre-oral and post-oral ciliary band, with an intervening tract of food groove cilia, extended around the periphery of each velar lobe. The shell at hatching stage (embryonic shell or protoconch I) consisted of slightly more than one whorl, had a punctated surface sculpture (Figure 1c), and was almost bilaterally symmetrical. When measured in lateral view from the outer lip of the aperture to the opposite side of the shell, protoconchs of hatching larvae had a mean value of 235.4 μm (SD 5.5 μm; n = 5). Rudiments of the cephalic tentacles were recognizable as a pair of stubby papillae at the apex of the larval body, and pigmented eyespots were visible through the transparent cephalic epidermis (Figure 1a). The larval heart was a thin-walled vesicle located beneath the floor of the mantle cavity that showed rhythmic contractions in hatching larvae, although contractions stopped when the foot and velum retracted into the shell. Occasional bouts of repetitive contractions in the area of the definitive heart were also evident in hatching larvae. These occurred slightly posterior to the larval heart. The strength and regularity of definitive heart contractions increased during the days following hatching, but the pe-

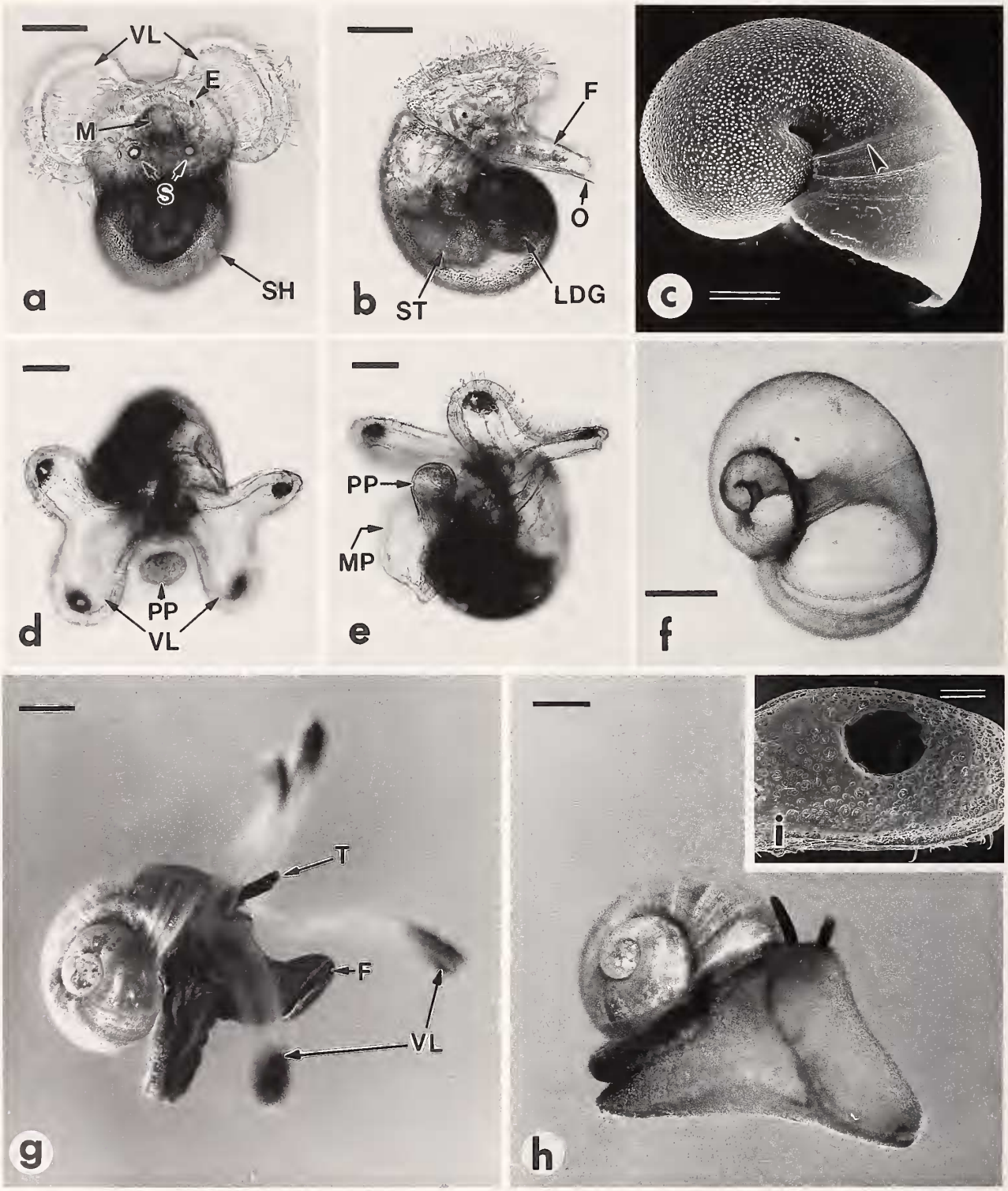

Figure 1

Larval and metamorphic development of *Polinices lewisii*. a. Newly hatched larva in antero-ventral view showing the two disc-shaped velar lobes (VL), shell (SH), eye (E), mouth (M), and statocysts (S); scale bar, 75 μm. b. Newly hatched larva in right lateral view showing the small foot (F) and operculum (O); the stomach (ST) and left digestive

riodicity was not synchronous with that of the larval heart.

Both the soft tissues and shell showed substantial growth between hatching and metamorphic competence (compare Figure 1b and g). Each of the enlarging velar lobes acquired two red pigment spots by 6 days post-hatching, and by 9 days each velar lobe began to bifurcate (Figure 1d, e). Eventually, the velum consisted of four long arms with a patch of red pigment embedded in both the upper and lower velar epidermis at the apex of each arm (Figure 1g). Formation of a four-armed velum and subsequent lengthening of each velar arm greatly increased the length of the velar ciliary bands relative to the initial bilobed condition.

Shell secreted during the larval stage (larval shell or protoconch II) had incremental growth lines but no surface punctae (Figure 1c). The growing larval shell spiraled in the orthostrophic direction (torsional asymmetry was dextral), which generated a low spire on the right and an umbilicus on the left (Figure 1f). At metamorphic competence, the shell had 2½ whorls and a mean diameter of 941 μm (SD 41 μm; n = 7) when measured from the outer lip of the aperture to the opposite side of the shell.

The foot of hatching larvae was a small, triangular extension of post-oral body wall that bore the operculum. At this initial larval stage, the foot had a low dorso-ventral profile along its entire length and lacked pigmentation (Figure 1b). The metapodial region of the foot began to spread laterally soon after hatching, but the most dramatic change in pedal form during the first third of larval life was the expansion of the propodium (Figure 1e). By 2 weeks post-hatching, the propodium was almost worm-like in shape and flexibility. After 2 weeks, the foot acquired the beginnings of the propodial and metapodial folds. Following metamorphosis, these folds enlarge sufficiently to almost completely cover the external surface of the shell; they function to prevent sediment from entering the mantle cavity during post-metamorphic burrowing behavior.

As the foot enlarged, there was a gradual accumulation of black pigment within the originally transparent pedal epidermis. Black pigment also appeared within the wall of the gut, within the epidermis of the head (excluding the velum), and within the floor of the mantle cavity. The mantle fold was sparsely pigmented, except for a strip of black that ran parallel to the developing osphradium. The black pigment strip became obvious approximately 3 weeks after hatching.

Other notable developmental events that we saw in whole mounts of live larvae included the elongation of cephalic tentacles, which occurred throughout the larval phase, and the appearance of gill lamellae along the roof of the mantle cavity at approximately 3 weeks post-hatching.

After approximately 5 weeks of laboratory culture, veligers of *P. lewisii* acquired the ability to crawl over surfaces or burrow into fine sediments using the darkly pigmented foot. When crawling began, the velar arms were retracted into the shell, and the remarkable foot of these late-stage veligers became greatly inflated so as to form a broad ventral platform beneath the shell. The inflation, together with the contours of the propodium, gave the leading face of the crawling foot a shovel-like shape (Figure 1h). As this highly maneuverable appendage was thrust into sediment during burrowing, cilia along the frontal slope of the foot generated a conveyor-belt-like transport of sediment particles from immediately in front of the foot, along the anterior face of the propodium, to the dorsal surface of the shell. The foot deflated rapidly and reverted to a shrunken condition when veligers stopped crawling or burrowing and either retracted fully into the shell or resumed swimming (Figure 1g).

Metamorphosis

Although we reared greater than 200 larvae of *P. lewisii* to metamorphic competence, some for a month past the onset of crawling ability, we identified only two cases of spontaneous metamorphosis in glass culture flasks containing coarse-filtered seawater. However, approximately 75% of larvae that were able to crawl underwent metamorphosis when placed in bowls of seawater containing approximately 1 cc of surface sediment from an area inhabited by adults (Patricia Bay site). Sediment that was autoclaved, then rinsed in filter-sterilized seawater, completely lost its inductive capacity. Pieces of *Ulva* were also ineffective for inducing metamorphosis of this gastropod. Small bivalves showed a modest capacity to induce metamorphosis of *P. lewisii*; three of 15 larvae metamorphosed in the presence of small bivalves of

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gland (LDG) are visible through the transparent shell; scale bar, 75 μm. c. Scanning electron micrograph of the shell from a young larva; arrowhead indicates the boundary between protoconch I and II; scale bar, 50 μm. d. Larva at 11 days post-hatching showing the propodium (PR) and initial bifurcation of velar lobes (VL); scale bar, 100 μm. e. Larva at 11 days post-hatching in left lateral view showing the enlarging metapodium (MP) and propodium (PP) of the foot; scale bar, 100 μm. f. Cleaned shell of a metamorphically competent larva showing 2½ shell whorls and orthostrophic coiling direction; scale bar, 250 μm. g. Metamorphically competent larva in right lateral view showing four long velar arms (VL), elongate cephalic tentacles (T), and large foot (F); scale bar, 250 μm. h. Young juvenile in antero-lateral view showing the shovel-like shape of the anterior face of the expanded foot; scale bar, 250 μm. i. Ostracod carapace drilled by a young juvenile of *P. lewisii*; scale bar, 100 μm.

mixed species composition that were isolated from Patricia Bay sediment.

Post-metamorphic individuals could be easily distinguished from crawling larvae because, during crawling behavior, the cephalic tentacles projected beyond the rim of the shell aperture only after the velar arms had been lost. The mechanism that destroys the velum was not observed directly because the velar arms were fully retracted into the mantle cavity during metamorphosis. However, we never observed discarded chunks of velar tissue or dissociated velar ciliated cells after competent larvae had been placed in sediment containing the inductive cue.

Between 3 to 5 days after loss of the velum, metamorphosed snails began feeding by drilling holes in shells of small, juvenile bivalves. Juvenile snails appeared to have an adhesive structure at the extreme posterior end of the foot because we occasionally saw juveniles crawling through sediment with a small bivalve attached to this area of the foot. Ostracods were abundant in the sediment samples that we used to induce metamorphosis of *P. lewisii* larvae, and these were also drilled and eaten by young, juvenile moon snails (Figure 1i).

DISCUSSION

The literature gives conflicting reports for the developmental pattern of *Polinices lewisii.* Giglioli (1955) predicted planktotrophic larvae for this species, based on embryo and capsule dimensions for egg masses collected from southeastern Vancouver Island at Ladysmith Harbour. However, Bernard (1967) reported that short-term, non-feeding larvae hatched from egg masses of *P. lewisii* collected from a slightly more northern site along eastern Vancouver Island at Departure Bay. Bernard's (1967) observations would seem more credible, since he actually observed hatching larvae of this species. He provided a sketch of an early, encapsulated veliger of *P. lewisii,* but did not illustrate hatching veligers. Nevertheless, Bernard (1967) stated that hatching *P. lewisii* larvae had a small velum but a large foot.

We found that *P. lewisii* egg masses collected from three locations around Vancouver Island (collections made during 4 successive years for the Patricia Bay site) released planktotrophic larvae. There are three possible explanations for this discrepancy in reports (1) Bernard (1967) was mistaken; (2) *P. lewisii* is capable of poecilogony (although a number of previous reports of poecilogony among gastropods have been disputed by Hoagland & Robertson [1988] and Bouchet [1989]); or (3) *P. lewisii* encompasses cryptic sister species that are distinguishable by a difference in developmental pattern only. The last possibility is not without precedent. Oliverio (1996) reviewed a number of such cases for caenogastropods from Europe. We hesitate to overthrow Bernard's (1967) interpretation because he describes a large foot for hatching larvae of *P. lewisii,* with the propodium developing within 24 hours. "Large" would not be an appropriate adjective for the foot of hatching larvae of *P. lewisii* that we observed (Figure 1b). Unfortunately, the site where Bernard (1967) collected *P. lewisii* egg masses has been destroyed by dredging for construction of a marine docking facility (Dr. Mary Arai, Pacific Biological Station, Nanaimo, British Columbia, personal communication). Nevertheless, it would be appropriate to intensively sample populations of *P. lewisii* along the west coast of British Columbia to test the hypothesis of cryptic sister species.

Our repeated failure to culture larvae of *P. lewisii* to metamorphic competence at 12°C was unexpected because this is within the normal summer temperature range for marine waters around southern Vancouver Island. At 3½ months, larvae cultured at 12°C appeared to be developmentally arrested at a stage corresponding to 60 to 70 percent completed development for larvae cultured at 20–22°C. By contrast, when larvae of an unidentified, subtidal naticid were cultured at 12°C and fed *Isochrysis galbana,* they showed a slow but consistent rate of growth and development, and they achieved metamorphic competence at 3 to 3½ months after hatching. Larvae of this unidentified species had a smooth protoconch I, unlike the sculptured protoconch I of *P. lewisii,* and they grew to a larger size at metamorphic competence than did veligers of *P. lewisii* (Pedersen, 1996). Our repeated failure to obtain a continuous progression of growth and development of *P. lewisii* larvae at 12°C, despite the fact that another species of naticid did well at this temperature, encourages us to believe that our inability to rear *P. lewisii* at 12°C may not be a laboratory artifact. Summer seawater temperatures in the shallow, protected embayments inhabited by adults of *P. lewisii* typically rise well above 12°C during the late spring and summer when egg masses are abundant. Data for Saanich Inlet show that summer temperatures of 15–20°C are routine for surface waters and shallow embayments (Dr. Louis A. Hobson, University of Victoria, personal communication). We speculate that larvae of *P. lewisii* may generally stay within the relatively warm bays where they hatch, and in fact, they may need these warmer temperatures to complete larval development.

Larvae of *P. lewisii* were induced to metamorphose by sediment from the intertidal zone of beaches inhabited by adults. The fact that sediment loses its inductive potency after autoclaving suggests that the active factor is organic, rather than some physical property of the sediment particles. The relatively small percent metamorphosis in the presence of bivalves alone might have been due to active factor in residual sediment or organic surface film adhering to the bodies of the bivalves. Unfortunately, we did not specifically test the ability of ostracods to initiate metamorphosis of *P. lewisii.* Until future experiments can narrow down the exogenous trigger for metamorphic induction, we tentatively propose that the active factor is

an indirect indicator of sites likely to harbor suitable small prey for *P. lewisii.*

Finally, our results do not agree with Bernard's (1967: 20) statement that young juveniles of *P. lewisii* feed on diatoms and *Ulva* until they are 5–6 mm in shell length, when they switch to predation on bivalves. We found that bivalves and ostracods were drilled and eaten by *P. lewisii* within 3 to 5 days of metamorphic loss of the velum. We found no evidence of feeding on *Ulva* when this was added to bowls containing young juveniles. Our observations are similar to those of Berg (1976), who reported that *Natica gualtieriana* is able to drill and ingest small gastropods shortly after metamorphosis. Kabat (1990) noted that the paleontological literature attributes boreholes in fossil ostracod shells to naticid predation. He therefore speculated that ostracods may be a "potentially important prey source for juvenile naticids." Our observations confirm that at least one species of extant naticid is an active predator of ostracods during its early post-metamorphic development.

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